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MIGRATION IN THE GRASSHOPPER *MELANOPLUS SANGUINIPES* (FAB.). I. THE CAPACITY FOR FLIGHT IN NON-SWARMING POPULATIONS

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Abstract

A tethered flight assay which identifies migratory behavior in the grasshopper *Melanoplus sanguinipes* (Fab.) was developed. The validity of the assay was examined by flight testing individuals collected at random from migratory and from virtually non-migratory field populations. Behavior in the tethered assay was found to accurately reflect the relative amount of migratory behavior in the field populations. Migratory flight appears to occur in this species even in the absence of obvious swarming behavior. Interpopulation differences in flight behavior observed in the field insects were maintained in first generation laboratory-reared progeny. Results of this study imply that migration is likely to play a significant role in the ecology of *M. sanguinipes,* even in nonoutbreak populations, and is not likely to be a simple facultative response to unusual environmental conditions.

Introduction

Migration has an integral role in the ecology of many species (Baker, 1978; Dingle, 1980; Lidicker and Caldwell, 1982). It may be an important factor limiting species range and distribution (Andrewartha and Birch, 1954) and is necessary if species are to invade and colonize new habitats. The frequency of migration is a major determinant of the rate of gene flow between two populations, and dispersal can stabilize populations in heterogeneous environments (Roff, 1974).

Understanding the significance of migration in a species' ecology requires a means of assessing its frequency of occurrence. However, with notable exceptions such as flights of the Monarch butterfly and swarms of the Middle Eastern locusts, the migrations of insects in the field are usually not apparent, and detection of long distance movement may require extraordinary effort. Even when insect movements are obvious or when attempts are made to assess the number of migrant individuals in a population, impressions of the extent of migration may be erroneous. For instance, reliance solely on observation of mass swarms alone can underestimate the frequency of migration in a species; individuals in nonswarming populations of the locusts *Schistocerca gregaria* (Forskal) and *Locusta migratoria* (R. et F.) also migrate (Davey, 1955, 1959; Roffey, 1963). Mark-recapture studies can provide information about the orientation and distances of movement, but may seriously underestimate the extent of migration if loss of individuals from the study population by death cannot be distinguished from loss due to emigration or if the appropriate life stage for migration is not chosen for study (Mallet, 1984). The difficulties of recapturing migrants that have moved significant distances from the point of release are compounded by a "dilution effect" as the area into which the organism has emigrated increases with the square of the distance

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moved (Southwood, 1966). Mark-recapture and other methods of identifying migrant insects that have been used in the field, such as radar detection or various means of trapping, are usually not practical for laboratory studies of such behavior.

The North American grasshopper, *Melanoplus sanguinipes* (Fab.), periodically engages in spectacular long distance mass migrations that can have serious economic impact on crops and rangeland. This swarming behavior, however, has been observed only rarely since the early 1900's and appears to be associated with unusual environmental conditions (Shotwell, 1930; Parker *et al.*, 1955; Scharff, 1961; Pfadt, 1982). Mark-recapture studies have suggested that nonswarming populations of *M. sanguinipes* are relatively sedentary (Riegert *et al.*, 1954; Baldwin *et al.*, 1958; Edwards, 1961). However, in these studies, recapture rates were quite low, and the authors could not distinguish death (with rapid removal of remains by scavengers) from emigration beyond the recapture search range. These studies implied that migration is extremely infrequent in this species, occurring only under extreme conditions. Based on such findings, it would seem that in the ecology of *M. sanguinipes* migration serves primarily as a means of escape from unfavorable conditions. We suggest, however, that earlier studies have greatly underestimated the frequency of movement in this species because of limitations of the field methods used to obtain estimates of migration. It is therefore desirable to attempt to examine the degree of migration in this species using a combination of field and laboratory methods. To that end we have employed a tethered flight assay in combination with field observation and have found that individuals migrate much more frequently than previous reports indicated. Indeed, although the proportion of migrants can vary greatly between populations, our results show that some individuals in all non-swarming populations may be migratory.

Materials and Methods

Flight assay

The tethered flight assay of Dingle (1965) was modified for use with *M. sanguinipes*. Grasshoppers were attached at the dorsal pronotum to a small lightweight stick using warmed Styx brand wax. Insects were suspended from a horizontal bar facing a fan generating a breeze of 11–13 km/h. Floodlights were used to increase the illumination and to raise the air temperature at the flight test station to 32–34°C. Flight tests were conducted between 3 and 12 hours after sunrise or lights-on. These conditions simulate those observed to be necessary for occurrence of migratory flights in the field (Parker *et al.*, 1955; Bird *et al.*, 1966) and flight in a wind tunnel (Riegert, 1962). Take-off was initiated by breaking tarsal contact or by moving the tethered animal rapidly through the air in a horizontal figure-8 pattern for several seconds. Test insects were allowed a maximum of five such take-off simulations or restarts during the flight test period (see Results). Total cumulative flight time was recorded. Occasionally, grasshoppers would hold wings outstretched without flapping. Only movement of both fore and hindwings was scored as flight.

Insects were flight tested within 24 hours of capture. Colorado field flight tests were conducted in a small mobile field lab. Arizona field flight tests were conducted either in a USDA facility in Phoenix or at the Bureau of Indian Affairs–Branch of Forestry in San Carlos.

Field collection and laboratory maintenance of grasshoppers

Insects used in field flight tests were collected from two areas in late July and early August. The first collecting area was a site 8.8 km north of Ted's Place (approximately

40°[illegible]05°10′W), Colorado (the CO population) along US Highway 287. The sec[illegible]an area approximately 1.6 km northeast of Cassadora Springs (approxi[illegible]24′N and 110°20′W) on the San Carlos Apache Indian Reservation, Arizona [illegible] population). Determination of the degree of migration at each site was based on published reports, observation of sustained flight, and behavior after release from confinement (described below). Grasshoppers from each field population were shipped to the University of Texas at Austin and used to establish separate colonies. Insects were reared in 30 × 30 × 30 cm screen and Plexiglas cages placed in Hotpack walk-in environmental chambers at 16L:8D photoperiod, 30–50% relative humidity, and 30°C. Fresh, washed lettuce and a mixture of 50:50 bran and wheat germ were available continuously. Growth chambers and cages were rinsed after each experiment in a 5.5% bleach solution followed by thorough hot water rinse. Cage design allowed feces and debris to drop through a screen floor onto a mat which was changed daily.

Containers of damp, sterilized sand were provided for oviposition. Egg pods were sifted from the sand and placed in moist vermiculite for at least 28 days at 30–32°C. Any eggs that had not hatched at the end of this incubation period and were not obviously diseased were assumed to be in diapause (Salt, 1949; Riegert, 1961) and placed in a cold room at 4–8°C for at least 3 months.

Results

Criteria for migratory flight in the laboratory tethered assay

To establish a practical laboratory assay for migratory behavior in *M. sanguinipes*, the tendency of AZ laboratory-reared individuals to initiate and maintain tethered flight was assessed. Each insect was allowed to fly until stopping itself, up to a maximum flight duration of 4 hours. Flight was monitored at 5-minute intervals (*i.e.*, 60 minutes represents animals that flew 56–60 min). Cuticle hardening was sufficient to allow flight by day 2 after adult emergence.

Insects ranged in age between 2–15 days post-eclosion and were tested on 2–3 separate occasions at least 3 days apart. In this experiment, performance in one flight test had little predictive value in a subsequent trial ($r^2 = 0.077$). Therefore the trials were assumed to be independent. The flight duration curve for the population was markedly skewed and is approximated by two distinct lines which intersect at the 60-minute interval (Fig. 1). Once the insect had flown 60 minutes it was much more likely to continue; 55% of the flights ended before the first hour, while 78% of the flights in progress at 60 min continued through the next hour. Although we have observed sustained flights of longer than 10 hours, we have not established an upper limit for flight duration in this species. As previously mentioned, grasshoppers were allowed a maximum of 5 take-off simulations during flight testing. This was necessary in part to compensate for disturbance of flight produced by the investigator when new grasshoppers were placed on the flight testing apparatus, although grasshoppers would also occasionally stop spontaneously. Short (less than 5 min) and intermediate (6–55 min) flyers stopped and were restarted more frequently ($x = 2.65$ times) before refusing to resume flight. Long flyers (flight longer than 60 min) stopped only an average of 1.25 times before cessation of flight (differences significant at $P < 0.001$, one-tailed t test). Thus, grasshoppers making flights in excess of 60 minutes were not only more persistent, but also were less easily interrupted than those making shorter flights. A flight time of 60 min or more is long enough for movement over a considerable distance or to reach regions of the atmosphere where transport by wind currents can occur (see Johnson, 1969). Sixty-minute flights are also quite distinct from the animal's

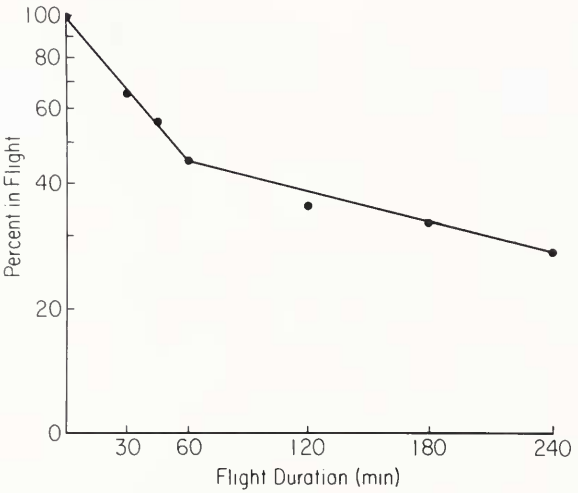

FIGURE 1. Semi-log plot of the percent of grasshoppers still in flight at given duration. Lines were drawn by sight. Data were recorded in 5-min intervals, *i.e.*, the 60-min point represents flights of 56 to 60 minutes. Flights still in progress at 4 hours were terminated. n = 16 males and 16 females with a total of 66 flights.

normal locomotor responses to vegetative or escape stimuli that usually evoke walking, hopping, or very brief flights of less than 2–3 seconds duration. Therefore, a flight duration of 60 minutes was chosen as the criterion for migratory behavior in *M. sanguinipes*, and in subsequent tests insects were stopped after they had flown one hour. The criterion was challenged by flight testing animals from field populations that exhibited different degrees of migratory behavior (see below).

Classification of field populations

Assessment of the migratory tendencies of field populations was based on several lines of evidence.

Published reports. Mass migrations had been observed at the AZ collecting area in early summer in both 1980 (Pfadt, 1982) and 1981 (Foster, pers. comm.), and marching hopper bands, characteristic of migratory locusts (Uvarov, 1966), were observed in 1980 and 1981 (Foster, pers. comm.).

There were no published reports of such activity at the CO site, although grasshopper populations had been monitored in 1980 and 1981 in conjunction with rangeland treatment programs.

Field observations of spontaneous flight activity. In the first week of August 1981 and in the last two weeks of July 1982, much spontaneous flight activity was observed in the AZ population during mid-day (10:00–16:00). The grasshoppers moved too rapidly to follow on foot. However, by standing motionless in an infested area (considered by agricultural entomologists to be a region with grasshopper densities = $8/yd^2$ or $8.81/m^2$) and scanning the horizon with 15× binoculars, we were able to detect sustained flights of at least 6 m above the ground which lasted more than 60 s and which carried the insect at least 50 m (beyond binocular range). These represent minimum possible estimates of the duration and distances covered by individuals; actual time in flight was certainly much greater. In contrast, at the CO site during two weeks each in late July 1980 and 1981 and two weeks at the end of July and beginning

of August 1982, sustained flights were not observed either while surveying the populations with binoculars or during sweep netting. The latter activity stimulated some movement of grasshoppers including escape flights but these lasted no more than 2–3 s and carried the insect at most 3 m. Attempts were made to quantify movement more precisely in each population with malaise net trapping and mark-recapture studies. However, the malaise trap proved to be an ineffective method for collecting flying grasshoppers and recapture rates were far too low to provide any estimate of death or emigration at either site.

Locusts, especially in the solitarious state, often migrate after sunset (Davey, 1955, 1959; Roffey, 1963), and, *a priori,* the high daytime temperatures and possible water loss problems at the AZ site would seem to favor nocturnal flight. Tethered flight tests made without lights during the animals' scotophase indicated that *M. sanguinipes* is capable of flight in the dark (McAnelly, 1984). However, in the course of nighttime observations either aided by flashlight or made when light levels (illumination from moonlight) were sufficient to detect small flying insects and to identify stationary and crawling insects, no movement of *M. sanguinipes* was detected in either field population. Although collections and scanning of fields with binoculars were done immediately after sunset and throughout the night, grasshoppers were quite immobile, usually roosting on vegetation. It may be that the temperature threshold for flight in this species is too high for nocturnal flight to occur frequently. Average daily minimum temperatures for July and August were less than 21.5°C in AZ and less than 15°C in CO (BIA-Forestry, San Carlos and Colorado Climate Center data). However, our observation period was quite limited (a total of 3 nights in AZ and 2 nights in CO), and we do not rule out the possibility of nocturnal flight in *M. sanguinipes* under appropriate conditions.

Flight of released animals. At each field site, resident grasshoppers were collected (n = approximately 40 at both sites) and confined in screen cages (with food available) for 3 days and then released on warm sunny days with light breeze. When AZ insects were released, all actively took flight and approximately 10% continued the flight beyond the range of binocular sight (50 m). No CO insects flew more than 1.0 m upon release while most slowly crawled out of the cage. Ambient temperature was well above flight threshold (29.4°C–Riegert, 1962) in both cases, though somewhat higher (41°C) in AZ than in CO (37°C).

Census data. Census data also revealed evidence of large scale population movements in AZ. At a site 1.6 km from Cassadora Springs in which we observed considerable spontaneous take-off activity, density was reduced from approximately 20 *M. sanguinipes*/m^2 (estimated by counting the number of grasshoppers flushed/m^2) to less than 1 grasshopper/m^2 within a 2-day interval. We observed no evidence of increased mortality or predation during this interval, suggesting almost total emigration from this site. Similar changes in local population density were not observed at the CO site (densities over a three-day period in one area averaged $13.3/m^2 \pm 3.3/m^2$).

Results of field flight tests

The validity of the stationary tethered flight assay for *M. sanguinipes* was tested by comparing flight performance of grasshoppers from the two field populations. Tethered flight tests conducted on field-collected animals revealed a highly significant difference in flight behavior between the AZ and the CO animals with AZ insects showing a much greater tendency to make long flights than CO animals (Table I). These results were consistent over a two-year period. Subdividing the 2×3 Chi square analysis for 1982 data into a 2×2 Chi square of short and intermediate categories (Snedecor and

TABLE I

Comparison of the flight performance of CO and AZ field populations in the stationary tethered flight assay

	1981		1982	
Flight duration (minutes)	AZ	CO	AZ	CO
0–5	17 (57%)	130 (86%)	43 (28%)	72 (49%)
6–55	7 (23%)	17 (11%)	66 (43%)	69 (47%)
56–60	6 (20%)	4 (3%)	43 (28%)	7 (5%)
Total	30	151	152	148
Percent migrants	20	3	28	5

Figures in parenthesis indicate the percent of total in each category (rounded to nearest whole percent).
1981: $2 \times 3\chi^2$ for 0–5 *versus* 6–55 *versus* 56–60 minute flights = 18.55, $P < 0.001$.
1982: $2 \times 3\chi^2$ for 0–5 *versus* 6–55 *versus* 56–60 minute flights = 33.27, $P \ll 0.001$. $2 \times 2\chi^2$ for 0–5 *versus* 6–55 minute flights = 3.35, $P > 0.05$.

Cochran, 1967) highlights the proportionately smaller contribution of the differences between short and intermediate flights (6–55 min) to the overall differences between populations. Therefore the main component of the difference in flight behavior between populations was, in fact, that due to flights longer than 60 min.

Flight behavior of laboratory-reared progeny

Difference in the flight behavior between the AZ and CO field populations has potentially important implications for the ability of this species to adapt to local conditions. However, it is first necessary to ascertain that the difference is actually due to interpopulation variability and not simply to differences in sampling. For instance, the decreased flight behavior observed in the CO population relative to the AZ population might be explained by differences in age or reproductive status of individuals at the two sites. Although exact age of the field animals could not be determined, dissection of field tested grasshoppers, indicated that reproductive differences did not account for behavioral differences (McAnelly and Rankin, 1986). Furthermore, the interpopulation differences observed in the field were retained in progeny reared under identical conditions in the laboratory (Table II). In this experiment, each individual was flight tested every day from day 2 post-eclosion until day 28. Both the number of "migrants" (defined as individuals which made at least one 60-minute flight) and the percentage of long flights made by "migrants" were determined. Significantly more AZ than CO grasshoppers were classified as "migrants" (Table IIA), and the AZ "migrants" made long flights significantly more frequently than those from the CO line (Table IIB). These results indicated that the interpopulation differences in migratory behavior are persistent and that short-term differences in environmental conditions between the AZ and CO habitats were not sufficient to account for the observed differences in migration.

Repeated laboratory flight testing identified a greater number of migrants than did single flight tests in the field for both populations (Table IIA). This would be expected when flight behavior of individuals is recurrent and variable over time (Davis, 1980). In this experiment, the percent of AZ or CO individuals making long

TABLE II

Comparison of flight performance of first generation lab-reared progeny from AZ and CO populations. Individuals were tested every other day from day 2 to day 28

Number of long flights	AZ	CO
0	16	27
1+	24	13
Percent migrants	60.0	32.5
$\chi^2 = 6.08, P < 0.02$		

A. Number of individuals making a long flight at least once. No difference was observed between the proportion of males and females that made at least one 60-minute flight. Therefore data from both sexes were combined. Nineteen female and 21 male AZ progeny and 18 female and 22 male CO progeny were tested.

	AZ	CO
Median score (%) of long flights in all trials made by "migrant" individuals	35.4	14.3
Range of scores	7.1–100%	7.7–66.7%
n	24	13
$z = 2.56, P = 0.0052$		

B. Comparison of the repeatability of long flight behavior of "migrants" from AZ and CO laboratory-reared progeny. The percent of long flights in all flight trials made by each individual is treated as a flight score. The scores for AZ and CO "migrants" were ranked and compared using the Mann-Whitney U for large samples, corrected for ties (Siegel, 1956). Within a population, there was no difference between males and females with regard to the percentage of long flights made by "migrant" individuals. Therefore data from both sexes were combined.

flights on any given day was similar to the percent recorded in single flight tests of the respective field populations. As a practical consideration in designing future experiments, we found that approximately 90% of the total number of migrants identified in 14 laboratory flight trials would have been identified in the first 5 trials.

DISCUSSION

Tethered flight assays have provided some of the best corroborating evidence of field observations. Long duration tethered flight has been correlated with evidence of migration in the field for several insect species (Dingle, 1965; Rose, 1972; Rankin and Rankin, 1980). Further, *Tetraopes* beetles caught in flight between two habitats performed significantly better in tethered flight tests than insects collected on the ground (Davis, 1981). However, to avoid circularity it is necessary that independent criteria of field migration are used in devising and verifying a laboratory assay for migratory behavior.

The most direct field test of a laboratory flight assay would be the flight testing of insects actually caught in the process of migrating as Davis (1981) has done. We were not able to collect grasshoppers in migratory flight in the current study, although this may be possible in the future if field conditions are favorable. However, several different lines of evidence were brought to bear on the problem of determining the relative degree of migration in two populations. Because *M. sanguinipes* is a serious crop pest,

populations are monitored regularly in both Colorado and Arizona. Thus we had independent assessments of the migratory tendency of both of our field populations for 1980–1982 in addition to our own observations. All of these criteria indicated a major difference in the amount of long-distance movement occurring in the two populations. Thus, these populations provided a real contrast in flight propensity with which to verify our laboratory assay.

Although the tethered assay clearly reflected the relative differences in flight behavior between AZ and CO insects, the exact correspondence between frequency of long-duration flight in the field and in tethered flight tests is difficult to assess. Some aspects of laboratory testing tend to overestimate while others underestimate actual flight in a field situation. For example, the proximate cues of warm temperature, light, wind speed (see Materials and Methods) known to be necessary for migration in both populations (Parker *et al.*, 1955; Riegert, 1962; McAnelly unpub. obs.) were provided during all flight tests, whereas field conditions are likely to be much more variable. On the other hand, in the field animals have the opportunity to fly any time conditions are appropriate, rather than only once every 2 or 3 days as in these experiments. Due to daily variability in individual flight performance, the likelihood that an insect will migrate increases with opportunity for flight. Thus given suitable conditions for flight every day, field animals might make migratory flights more frequently than indicated by the laboratory assay. Conversely, the flight test includes the artificial impetus of a simulated take-off which could inflate the laboratory estimate by obviating any take-off threshold that might limit numbers of migrants in the field. Analysis of the tethered flight behavior of grasshoppers actually caught in migratory flight may eventually allow more precise quantitative estimates of the numbers of field migrants.

Both field observations and flight assay results indicated that there were substantial numbers of migrant individuals in the AZ population even in the absence of mass swarming. The fact that flight test results from the CO population identified 3–5% of the individuals as migrants underscores the difficulty, discussed previously, of relying solely on field observations to estimate the numbers of migrants and suggests that even in a relatively sedentary population of *M. sanguinipes* there are some migratory individuals. Observations of *M. sanguinipes* in Colorado at altitudes above its normal range or trapped in snowbanks have been made annually and support the conclusion that a fraction of the CO population is migratory even in non-outbreak years (Alexander, 1964).

The finding that there are striking differences in migratory behavior between populations has important implications for any study of the biology of *M. sanguinipes*. The interpopulation variation in migratory behavior between the AZ and CO populations is associated with marked differences in habitat quality between the two sites. The high degree of migratory activity at the AZ site is likely to be a response to semi-arid conditions and patchy distribution of resources at this site (Southwood, 1962; McAnelly, 1984, 1985). The CO field and lab insects were clearly less migratory than the respective AZ grasshoppers, presumably reflecting the relatively more lush and uniform habitat at the CO site (McAnelly, 1984). Alexander (1964) has suggested that the limited movements of individuals to high-altitude Colorado habitats that are only occasionally suitable for completion of the life cycle serve to allow immediate expansion of range during favorable years.

The causal basis for these differences has important consequences for the means by which mass swarms develop and for the ability of this species to invade and exploit new habitats. Retention of differences in flight propensity in the first generation laboratory-reared progeny suggests that immediate environmental conditions experienced by the individual are insufficient to explain the interpopulation variation in migration.

The experiments described in this study do not allow us to distinguish between the possible influence of environmental factors experienced by the parents (*i.e.,* maternal effects) and the role of genotype in determining whether an individual becomes a migrant. However, subsequent work has indicated that migratory behavior is under strong genetic control in this species (McAnelly, 1984, 1985; Rankin *et al.,* 1986; McAnelly and Rankin, in prep.), suggesting that the geographic variation in flight behavior and temporal changes in the proportions of migrants within a population may be at least in part the result of differential selection. Thus, even a very low proportion of migrants could play a significant role in the biology of the CO population by providing the necessary variation upon which selection could act to shift the balance toward a greater degree of migratory behavior as environmental conditions change over time (McAnelly and Rankin, in prep.; Parker *et al.,* 1955; see also Danks, 1983).

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